

Ontogenetic niche changes in haddock *Melanogrammus aeglefinus* reflected by stable isotope signatures, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

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ABSTRACT: We investigated stable nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotope signatures in haddock *Melanogrammus aeglefinus* in Ullsfjord, Norway, and found evidence of an ontogenetic shift as a result of growth but in the absence of other morphological changes. Stable isotope signatures and trophic level (TL) changed significantly from a pelagic signature and a low TL to a more benthic associated signature and higher TL when the fish were ca. 20 cm in length. The stable isotope signatures of haddock were compared with those of Atlantic cod *Gadus morhua* from the same system, other main demersal fish species in the fjord, and haddock from the adjacent fjord, Sørfjord. Our results indicate that both haddock and cod are opportunistic feeders, feeding on the abundant crustaceans in the fjords. Several of the large demersal fish species in Ullsfjord had very similar stable isotope signatures, which reflected their predation on similar prey types.

KEY WORDS: Diet · Demersal fish · Gadoids · Feeding ecology · Trophic level · Young-of-the-year

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INTRODUCTION

Our understanding of life history traits as well as interactions of prey and predatory species is important for fisheries management. As we move towards improving fisheries management through ecosystem-based management, knowledge of size-based feeding changes is essential for understanding food webs. High latitude ecosystems are relatively low in diversity and a few top predators are thought to drive the ecosystem through top-down control (Frank et al. 2007). Haddock *Melanogrammus aeglefinus* is one of the major commercial species in the North Sea, Barents Sea and off the coast of Norway. Recent years the spawning stock biomass (SSB) of northeast Arctic haddock in the Barents Sea and off the coast of northern Norway has been increasing, and for 2012 it is expected to be at a record high of 413 000 t (ICES 2011). While the oceanic offshore northeast Arctic stock of Atlantic

cod *Gadus morhua* is historically large, the SSB and recruitment (age 3) of the coastal cod stock inhabiting coastal and fjord areas is at a historical low (ICES 2011). Cod and haddock are therefore important in this region both as predators with top-down effects as well as for direct exploitation.

Ullsfjord is a high latitude fjord ecosystem at 70° N in northern Norway. The fjord supports small-scale local fisheries common in fjords along the Norwegian coast. The main target species are Atlantic cod, deep-water shrimp *Pandalus borealis*, haddock and saithe *Pollachius virens*, but less exploited demersal fish species also inhabit the Ullsfjord ecosystem, including long rough dab *Hippoglossoides platesoides*, whiting *Merlangius merlangus* and witch flounder *Glyptocephalus cynoglossus* (Nøstvik & Pedersen 1999). Young-of-the-year (YOY) haddock in the size range of 10 to 20 cm have high biomasses in Ullsfjord and are assumed to be important prey for large predatory fish and seabirds (Bugge et al. 2011).

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Both haddock and cod have small eggs and pelagic larvae and therefore change from a pelagic niche to a more demersally associated niche in larger fish as they grow (Bergstad et al. 1987). Haddock settle in the demersal habitat when they are between 4 and 14 cm, and cod settle at 4 to 8 cm (Robb & Hislop 1980, Godø et al. 1989). At this stage the diet of haddock is reported to change from pelagic copepods to demersal prey such as mussels, polychaetes and small fish as they settle in deep waters, while coastal cod continue to eat pelagic prey like copepods and settle in inshore waters (Demain et al. 2011). By changing their habitat or diet through life young individuals can maximize their fitness by reducing intraspecific competition and predation from other predatory fish as well as from larger conspecifics (Werner & Gilliam 1984). Several studies have suggested that inter- and intraspecific competition may be a driver of resource use and niche diversification (e.g. Svanbäck & Bolnick 2007, Shaw et al. 2008).

Stable isotopes in tissues of marine organisms reflect the diet of consumers and their analysis is becoming a widely accepted and applied tool for determining food web structure and carbon flow in ecosystem ecology (e.g. Fry 1988, Hobson et al. 2002, Nilsen et al. 2008). The nitrogen isotope ratio ($\delta^{15}\text{N}$) is used as an indication of the trophic level (TL) of the animal (Cabana & Rasmussen 1996) because tissue $\delta^{15}\text{N}$ values increase up the food chain. A mean fractionation factor of 3.4‰ per trophic level has been estimated (Minagawa & Wada 1984, Post 2002). The carbon isotope ratio ($\delta^{13}\text{C}$) is used to determine whether the food source is linked to the pelagic or benthic zone (Peterson & Fry 1987, Hobson & Welch 1992, Post 2002). Carbon originating from pelagic phytoplankton has a low (highly negative) $\delta^{13}\text{C}$, while the benthic and littoral zones are more enriched in ^{13}C (less negative $\delta^{13}\text{C}$). Because the trophic fractionation of $\delta^{13}\text{C}$ is small (0 to 1‰ per TL) (Hobson & Welch 1992, Post 2002) this can be used to separate primary sources of carbon. The isotopic niche refers to the area of a $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot occupied by one species (Newsome et al. 2007).

Most work on early life feeding of gadoids has been based on traditional stomach sampling (e.g. Pedersen & Fossheim 2008, Dalpadado et al. 2009); this is a time-consuming method that only provides a 'snapshot' of what has been recently consumed. In this study we present data from recently collected samples of the predatory fishes from Ullsfjord, with a main focus on haddock. Our objectives were to investigate whether stable isotope signatures (1) of haddock and cod varied with size within species,

(2) differed between haddock and cod, (3) differed between other demersal species in Ullsfjord and (4) differed between haddock with different geographic distributions.

MATERIALS AND METHODS

Sampling and stable isotope analysis

Sampling was done from RV 'Johan Ruud' (University of Tromsø) at 5 locations in Ullsfjord within 1 wk in February 2010. Demersal fish species were collected by bottom trawl with a Campelen shrimp trawl that had a circumference of 1300 meshes, equipped with rockhopper gear and a 20 mm inner net mounted in the cod-end. Trawling duration was 20 min and average speed was 2 knots (3.7 km h^{-1}). Pelagic-feeding copepods, *Calanus finmarchicus*, were collected by a WP2 plankton net (180 μm mesh) at the same stations and the haul was pulled through the whole water column. *C. finmarchicus* were collected to use as a baseline for the pelagic food web. The depth of the stations varied from 120 to 425 m (Fig. 1). Individual biometric measurements such as length, weight and sex were recorded for the fish samples. Muscle samples of about 1 to 2 cm^3 were taken from the area between the head and first dorsal fin, above the lateral line of each fish. For *C. finmarchicus*, whole animals were used for analysis. All samples were frozen at -18°C until further analysis. In the laboratory the skin was removed from the fish muscle, and the samples were rinsed in distilled water before they were dried at 60°C for 48 h, subsequently ground into a fine powder with a mortar and pestle and stored in microcentrifuge tubes at -18°C until further analysis. *C. finmarchicus* samples were treated with 2 N HCl before spectrometry analysis to remove non-dietary carbon in the exoskeleton. The mass spectrometry analysis for determination of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ was conducted at the Institute for Energy Technology (IFE), Kjeller, Norway, with a Nu Horizon isotope ratio mass spectrometer (Nu Instruments). Stable isotope ratios are expressed in δ notation as deviation in parts per thousand (‰) from a standard material, Pee Dee belemnite limestone for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$.

Because lipids are depleted in ^{13}C relative to ^{12}C , the carbon isotope values ($\delta^{13}\text{C}$) of lipid-rich animals such as copepods will be strongly negative. As lipid removal was not done chemically we used regression Eq. (1) (Post et al. 2007) to normalize for the effect of

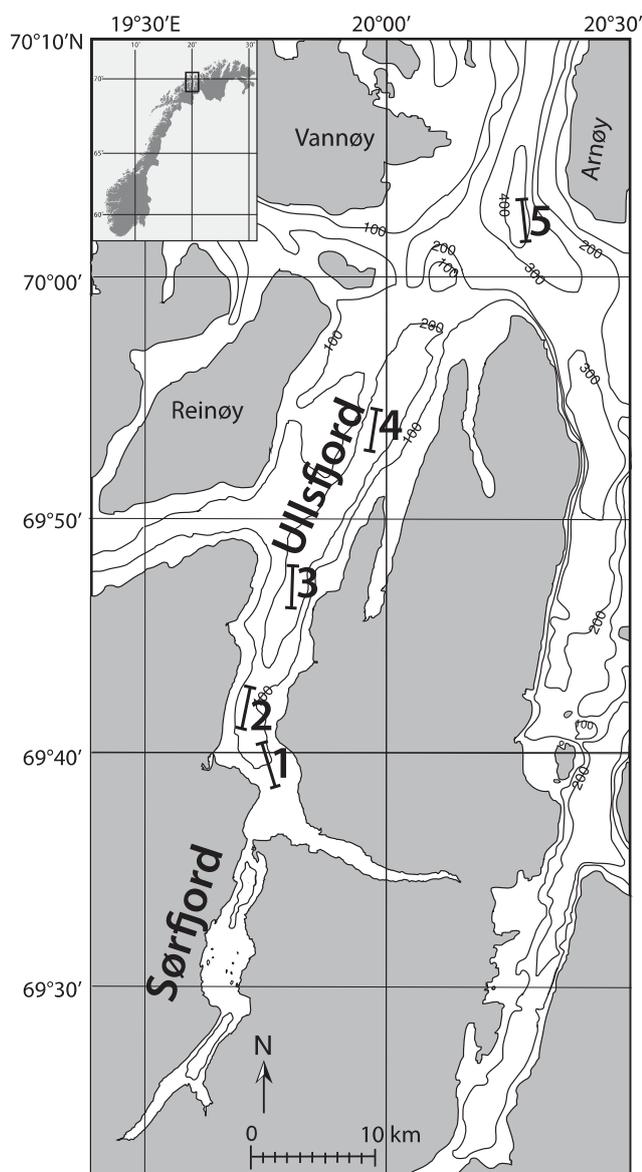


Fig. 1. Sampling area in Ullsfjord, northern Norway. The trawling grounds are marked as bars. Average depths are (1) 125 m, (2) 120 m, (3) 270 m, (4) 275 m and (5) 425 m

lipids, and Eq. (2) (Abrantes et al. 2012) to calculate the amount of lipids in the samples.

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times \text{C:N} \quad (1)$$

$$\text{Lipids (\%)} = -16.53 + 6.27 \times \text{C:N} \quad (2)$$

Haddock had an average C:N ratio of 3.16 (SD, 0.06). This is equivalent to a lipid level of 3.29% according to Eq. (2). For marine animals with a lipid level <5% it is not necessary to remove or convert the $\delta^{13}\text{C}$ values to account for lipids (Abrantes et al. 2012). The C:N ratio was weakly correlated with fish

length (Spearman's rank correlation: $r_s = 0.38$, $p < 0.001$). However, for comparative reasons with other studies, and because 2 witch flounders had a C:N ratio above 5 we chose to convert all values. This was done so treatment would be the same for all values when comparing them statistically.

TL was calculated from the following equation:

$$\text{TL} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}}) / \Delta\delta^{15}\text{N} + \text{TL}_{\text{base}} \quad (3)$$

where $\delta^{15}\text{N}_{\text{consumer}}$ is the $\delta^{15}\text{N}$ of the group or species in question, and $\delta^{15}\text{N}_{\text{base}}$ and TL_{base} are the $\delta^{15}\text{N}$ and TL values of the baseline species, respectively. We selected the herbivorous copepod *Calanus finmarchicus* and assumed it had a TL of 2.0 (Petursdottir et al. 2008). $\Delta\delta^{15}\text{N}$ is the trophic enrichment factor per TL, and we chose to use 3.4‰ as this has been suggested as an average enrichment factor (Minagawa & Wada 1984, Post 2002).

Statistics

All the figures and statistical analyses were made by using the R software (<http://cran.r-project.org/>). Because the data did not show homogeneity of variance when tested with a Brown-Forsythe Levene-type test (BF Levene), non-parametric tests were chosen to test for differences between length groups and between species. Two groups such as haddock and cod were tested by using the Wilcoxon rank sum test with continuity correction (WR_c). When testing whether stable isotope values differed between length groups within one species, the non-parametric Kruskal-Wallis rank sum test (KW) was chosen. A pairwise comparison using the Wilcoxon rank sum test with Bonferroni correction (WR_B) was used as a post hoc test to investigate which length groups were significantly different. For correlation tests we used Spearman's rank correlation (r_s). Frequency plots were used to show the distribution of the isotope signatures within one species and the overlap between species. The area under the curve is standardized to 1.

RESULTS

Haddock displayed large variances in stable isotope values but had low $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures at small fish lengths (20 cm and smaller), and a more enriched signature of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at larger sizes (Fig. 2a,b, Table 1). When we divided the haddock into length groups, the smallest group (10 to 20 cm)

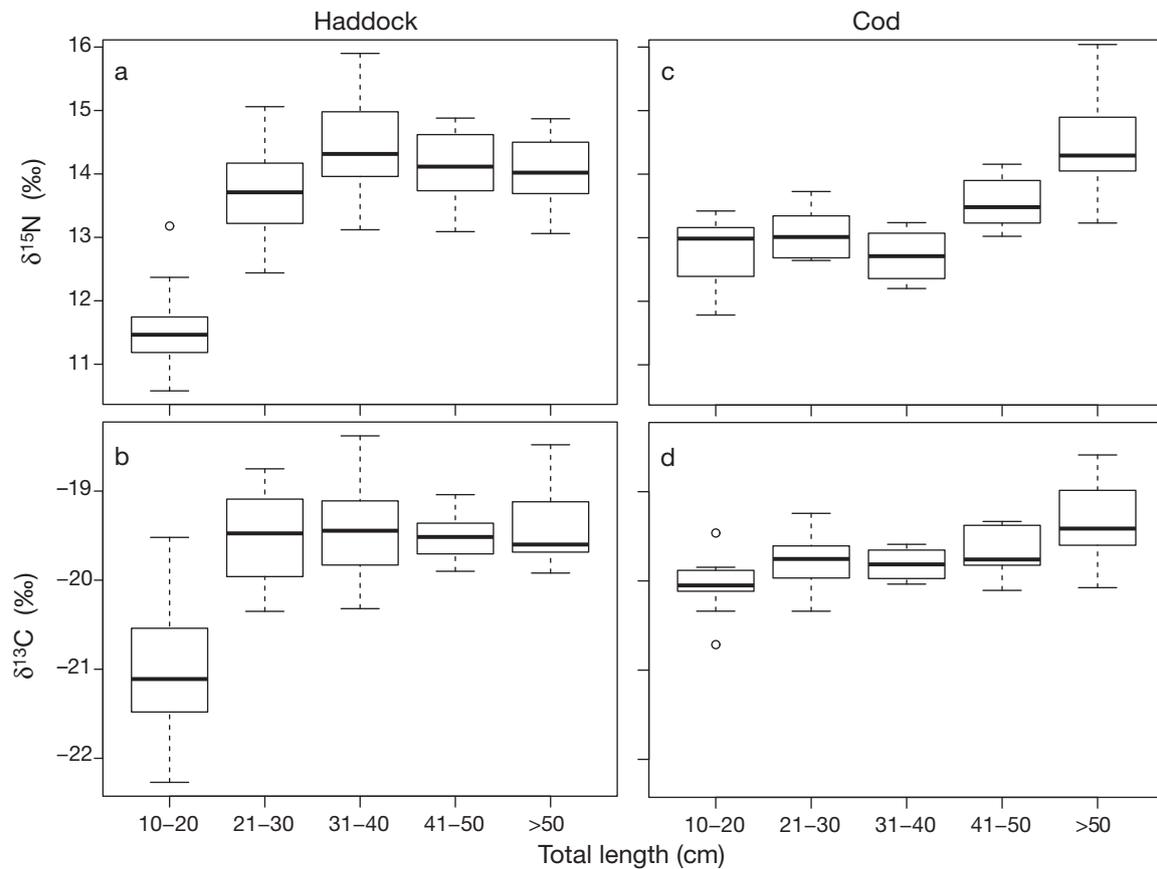


Fig. 2. *Melanogrammus aeglefinus* and *Gadus morhua*. Comparison of isotope signatures of the different length groups of haddock and cod: (a) $\delta^{15}\text{N}$ haddock, (b) $\delta^{13}\text{C}$ haddock, (c) $\delta^{15}\text{N}$ cod and (d) $\delta^{13}\text{C}$ cod. Box plot shows median (solid thick line), 25th and 75th quantiles (box) and minimum and maximum values excluding outliers (whiskers). Circles indicate possible outliers. See Table 1 for sample sizes (n)

Table 1. Mean length per length group (for haddock and cod), mean (\pm SD) stable isotope signatures $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, C:N ratio and trophic level (TL) for haddock *Melanogrammus aeglefinus*, cod *Gadus morhua* and main demersal species in Ullsfjord, Norway. $\delta^{13}\text{C}$ values are lipid-corrected using Eq. (1) and TL was calculated according to Eq. (3). n: number of observations

Species	Length group (range, cm)	Mean length (cm)	Mean $\delta^{15}\text{N}$ (\pm SD)	Mean $\delta^{13}\text{C}$ (\pm SD)	C:N ratio	TL	n
<i>Melanogrammus aeglefinus</i>	16–75	28.83	12.96 (\pm 1.42)	-20.13 (\pm 0.96)	3.16	3.16	75
	10–20	17.97	11.51 (\pm 0.53)	-21.03 (\pm 0.65)	3.13	2.73	32
	21–30	25.78	13.78 (\pm 0.72)	-19.50 (\pm 0.53)	3.19	3.40	18
	31–40	35.00	14.45 (\pm 0.81)	-19.43 (\pm 0.57)	3.17	3.60	10
	41–50	45.88	14.11 (\pm 0.61)	-19.51 (\pm 0.27)	3.17	3.50	8
	>50	58.00	14.04 (\pm 0.66)	-19.37 (\pm 0.50)	3.18	3.48	7
<i>Gadus morhua</i>	10–106	45.39	13.67 (\pm 0.92)	-19.61 (\pm 0.44)	3.18	3.37	58
	10–20	13.50	12.94 (\pm 0.61)	-20.06 (\pm 0.32)	3.27	3.10	10
	21–30	25.90	13.11 (\pm 0.44)	-19.77 (\pm 0.33)	3.18	3.20	11
	31–40	34.25	13.42 (\pm 1.03)	-19.81 (\pm 0.20)	3.15	3.09	4
	41–50	44.43	13.69 (\pm 0.55)	-19.66 (\pm 0.30)	3.15	3.33	7
	>50	68.08	14.34 (\pm 0.67)	-19.33 (\pm 0.40)	3.15	3.60	26
<i>Hippoglossoides platessoides</i>	25–34	29.00	14.01 (\pm 0.59)	-19.01 (\pm 0.28)	3.09	3.47	5
<i>Merlangius merlangus</i>	24–34	28.58	14.14 (\pm 0.35)	-19.45 (\pm 0.21)	3.09	3.50	19
<i>Glyptocephalus cynoglossus</i>	25–46	38.63	14.05 (\pm 0.42)	-18.38 (\pm 0.43)	3.28	3.48	27
<i>Calanus finmarchicus</i>			9.03 (\pm 0.13)	-19.90 (\pm 0.57)	7.29	2.0	15

was significantly different from all the other length groups (KW, WR_B : $p < 0.01$ for $\delta^{15}N$ and $\delta^{13}C$). Mean $\delta^{13}C$ for the smallest group (10 to 20 cm) of haddock was -21.03% , while the mean for the second smallest group (21 to 30 cm) was -19.50% . The mean $\delta^{15}N$ of the smallest group was 11.51% and the second group had a mean of 13.78% . The $\delta^{15}N$ and $\delta^{13}C$ values were highly correlated ($r_s = 0.90$). The smallest group of haddock was distinct from the larger ones in the isotope bi-plot (Fig. 3). The distribution for $\delta^{15}N$ values was bimodal with modes of about 11.5% and 14% , respectively (Fig. 3).

Cod had no marked shift in stable isotopes with increasing length (Fig. 2c,d). $\delta^{15}N$ and $\delta^{13}C$ signatures for cod in the 10 to 20 cm size group were significantly different from cod > 40 cm (KW, WR_B : $p < 0.01$) but not from those between 21 and 40 cm. For cod and haddock of 10 to 20 cm length both isotopes differed between species (Fig. 4). The small haddock (10 to 20 cm) were depleted in both ^{15}N (WR_C : $p < 0.001$) and ^{13}C (WR_C : $p < 0.001$) compared with those of cod. For larger cod and haddock the stable isotopes signatures were very similar (Fig. 5).

In addition to cod and haddock, we investigated several other demersal fish species in Ullsfjord. For comparisons between species we used individuals in

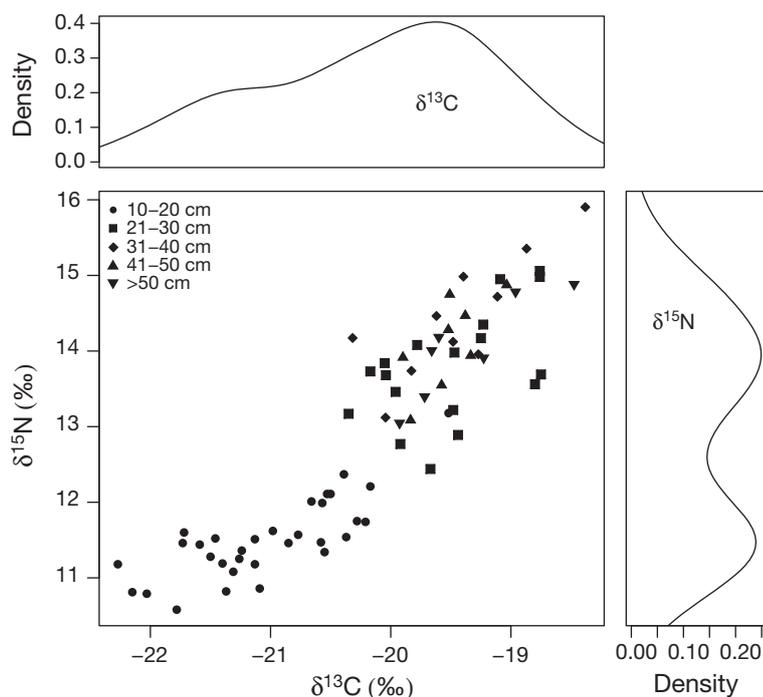


Fig. 3. *Melanogrammus aeglefinus*. Scatterplot showing haddock $\delta^{13}C$ and $\delta^{15}N$ values ($n = 75$). The distribution of the values along the axes are shown in frequency plots. $\delta^{13}C$ is shown above the scatterplot and $\delta^{15}N$ is on the right

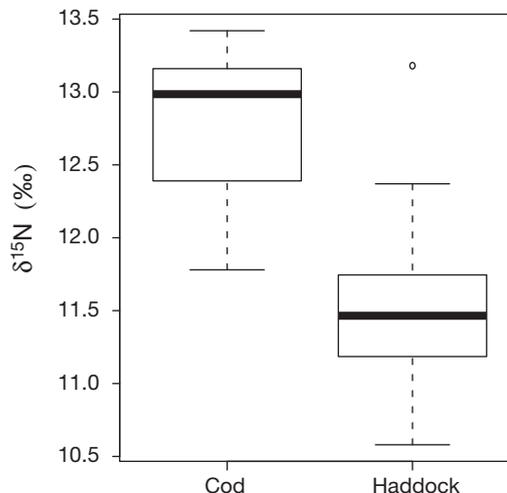


Fig. 4. *Gadus morhua* and *Melanogrammus aeglefinus*. Comparison of $\delta^{15}N$ for cod ($n = 10$) and haddock ($n = 32$) for fish lengths of 20 cm and smaller. See Fig. 2 for description of box plots

the size range of 25 to 45 cm from haddock and cod to match the size range for which we had samples from whiting, long rough dab and witch flounder. The demersal species showed large overlaps in both $\delta^{13}C$ and $\delta^{15}N$ signatures (Figs. 6 & 7). Witch flounder had significantly higher $\delta^{13}C$ than did the other demersal species we sampled, and $\delta^{13}C$ in long rough dab was significantly higher than in cod (WR_B : $p < 0.05$). There was no significant difference in $\delta^{13}C$ between cod and haddock, cod and whiting, haddock and long rough dab, haddock and whiting or whiting and long rough dab. However, for cod in the size range of 25 to 45 cm $\delta^{15}N$ was significantly lower than in haddock, whiting and witch flounder (WR_B : $p < 0.05$), while no statistical difference in $\delta^{15}N$ signatures was apparent in the other species.

After conversion (Eq. 1), the values of $\delta^{13}C$ samples that had a C:N ratio under 3.32 (low in lipids) became slightly more negative. For haddock the $\delta^{13}C$ decreased on average by 0.19 (SD, 0.06; range, 0.06 to 0.32). For cod the $\delta^{13}C$ decreased on average by 0.18 (SD, 0.07; range, 0.02 to 0.29). In contrast, for the lipid-rich copepod *Calanus finmarchicus*, which had an average C:N ratio of 7.3, the values of $\delta^{13}C$ increased by an average of 4.21 (SD, 0.91; range, 5.67 to 2.63).

Haddock was at the lowest overall average TL for the fish species at 3.16 and

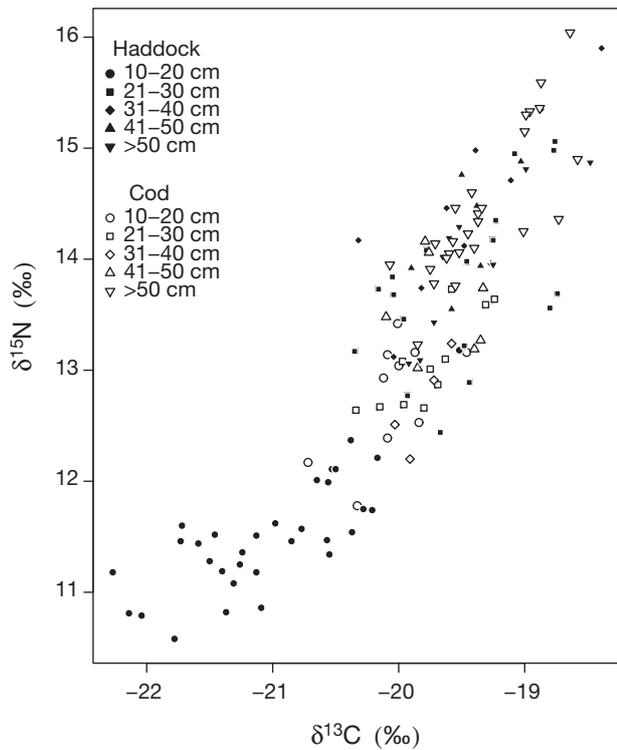


Fig. 5. *Gadus morhua* and *Melanogrammus aeglefinus*. Scatterplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope signatures for cod (n = 58) (open symbols) and haddock (n = 75) (solid symbols)

whiting was at the highest at TL 3.50 (Table 1). The smallest group of haddock was at TL 2.73, the lowest of all groups, while haddock in the length group of 31 to 40 cm was at TL 3.60, the same as the largest group of cod (>50 cm).

DISCUSSION

Ontogenetic niche shift and size-dependent niche diversification

We can interpret the change in $\delta^{13}\text{C}$ in haddock between the 10 to 20 cm group and the 21 to 30 cm group to be a result of a change in diet from pelagic to more demersally associated prey. This ontogenetic change in isotopic values has to our knowledge not been described previously. An abrupt change in diet and habitat can correspond to the metamorphosis from larvae to juveniles in, for example, largemouth bass *Micropterus salmonides* (Post 2003), yellowfin tuna *Thunnus albacares* (Graham et al. 2007) and red snapper *Lutjanus campechanus* (Wells et al. 2008). However, abrupt changes in diet as a result of increased size, but otherwise no morphological

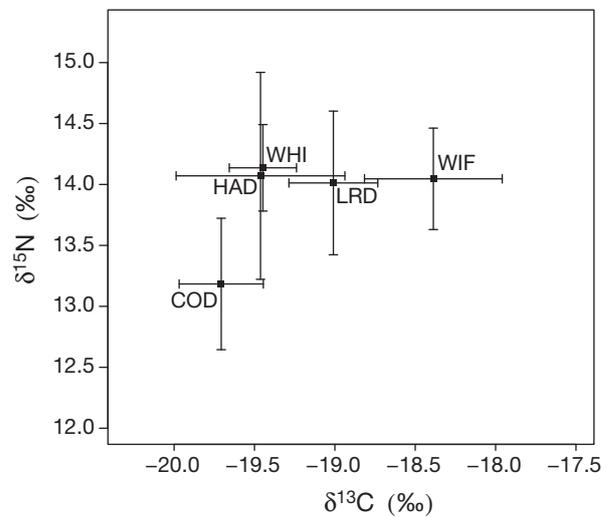


Fig. 6. Demersal fish species' stable isotope signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) displayed with means (solid squares) and error bars representing ± 1 SD. HAD: haddock *Melanogrammus aeglefinus* (25 to 45 cm); COD: cod *Gadus morhua* (25 to 45 cm); WHI: whiting *Merlangius merlangus*; LRD: long rough dab *Hippoglossoides platessoides*; WIF: witch flounder *Glyptocephalus cynoglossus*

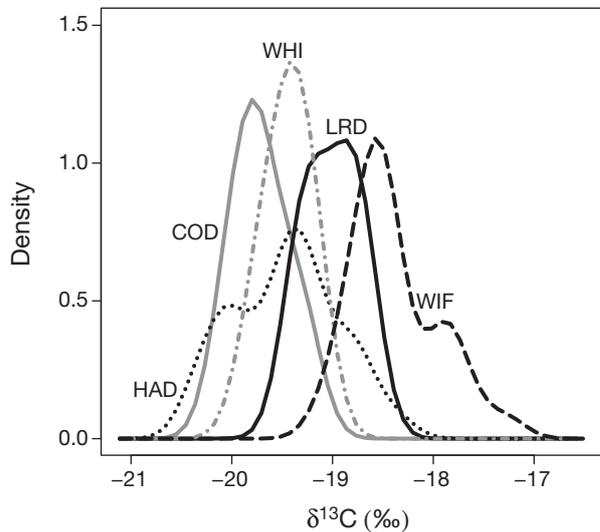


Fig. 7. Overlap in $\delta^{13}\text{C}$ among demersal species in the Ullsfjord system plotted in a frequency plot. Species abbreviations as in Fig. 6

change, are not well described. Small haddock in Ullsfjord were more depleted in ^{13}C than were larger fish, which indicates they feed on prey more connected to the pelagic zone.

The turnover time of isotopes in the muscle will be shorter in younger and faster-growing individuals than in larger, slow-growing fish. YOY haddock will increase their body mass about 9 times as they grow;

they settle at about 10 cm in size in August to October (Godø et al. 1989, Dalpadado et al. 2009) and grow to 20 cm at about 1 yr of age the next spring. Weidel et al. (2011) found the half-life of $\delta^{13}\text{C}$ in 0-age-group freshwater species to be from 8 to 18 d. Although the haddock in our survey were larger than the juveniles examined by Weidel et al. (2011), the growth of haddock and cod is so fast during the first year that the isotopes found in the muscle are a reflection of the diet within a relatively short time span. Also, if the observed signatures did originate from when the fish were in the pre-settlement stage, we would expect the same signature from the YOY cod, but this was not the case.

The difference in TL value for haddock was 0.75 TL from the smallest to the largest length group. The 31 to 40 cm size group had a TL of 3.60 meaning it was 0.86 TL higher than the smallest group. The bimodal distribution of haddock $\delta^{15}\text{N}$ corresponds to the 2 size groups: small haddock (≤ 20 cm in length) and larger haddock (> 20 cm). The TL of the smallest group is below 3.0, which indicates that they feed at least partly on prey that have lower $\delta^{15}\text{N}$ values than does *Calanus finmarchicus*. As we assume small haddock do not feed on phytoplankton, the likely prey items for the YOY haddock are euphausiids, amphipods and copepods. Some amphipods have very low $\delta^{15}\text{N}$, for example the genus *Gammarus* in the adjacent Sørfjord (Nilsen et al. 2008) and amphipods from kelp forests (Fredriksen 2003). This could partly explain the low $\delta^{15}\text{N}$ in YOY haddock. It is no surprise that predatory fish feed at higher trophic levels when they increase in size because as they grow they can feed upon larger prey, and the range of possible prey generally increases with size (Cohen et al. 1993, Jennings et al. 2002). Shifts from planktivory to piscivory have been described for many species (Post 2003, Graham et al. 2007), and haddock in Ullsfjord may shift from feeding on small pelagic zooplankton, euphausiids and amphipods to larger crustaceans such as the abundant shrimp species *Pandalus borealis* and *Pasiphea multidentata*, as well as benthic invertebrates and small fish. Further investigations are necessary to precisely determine the prey species of haddock.

The slightly more negative $\delta^{13}\text{C}$ values after correction for lipids (Eq. 1) may contribute to some misinterpretations. The $\delta^{13}\text{C}$ signature of the smallest group of haddock even became more depleted than that of the herbivorous copepod *Calanus finmarchicus*, and it is difficult to interpret whether this is an effect of the conversion method or if the haddock feed on prey that have more depleted isotope signatures. The

smallest group of haddock had, on average, a lower C:N ratio compared with the other groups and this led to increased difference between the size groups. However, the trends from the results were the same when non-corrected values were used in the comparisons and therefore the conversion method does not influence the conclusions of the study.

Trophic level calculations

The baseline for TL calculations, the copepod *Calanus finmarchicus*, was assumed to be a strict herbivore at TL = 2 as described in Nilsen et al. (2008). However, $\delta^{15}\text{N}$ and the TL of *C. finmarchicus* can vary throughout the year (Søreide et al. 2006). Also, from Trondheimsfjorden farther south in Norway, Saage et al. (2008) found that *C. finmarchicus* had an average TL of 2.4 and the highest $\delta^{15}\text{N}$ in this copepod occurred in February before the spring bloom started. Thus, the assumption that our baseline organism, *C. finmarchicus*, is found strictly at TL 2.0 may be questionable. If a TL of 2.4 was used, the TL of all fish would increase by 0.4 TL, giving the smallest group of haddock a TL of 3.05 and whiting a TL of 3.74. For the enrichment factor ($\Delta\delta^{15}\text{N}$) we chose to use 3.4‰ as this value is a good overall average (Minagawa & Wada 1984, Post 2002). However, Sweeting et al. (2007) suggested using 3.2‰ for investigations where fish muscle was sampled, as in this study, while Hobson & Welch (1992) suggested 3.8‰ as an overall average fractionation factor. Changing the $\Delta\delta^{15}\text{N}$ to 3.2‰ or 3.8‰ would give the same trend; the smallest group of haddock would still be below a TL of 3.0.

Comparison with other demersal fish species

The abrupt change in both carbon and nitrogen isotopes with increasing length was not displayed by cod, which suggests that the small haddock occupy a different niche from both large haddock and small and large cod (Figs. 4 & 5). It is important to note that all samples were collected from bottom trawls at depths of 125 to 425 m, and it is likely that some small cod use the sublittoral zone as a nursery area (Berg & Pedersen 2001). For large cod and haddock the stable isotope signatures overlapped almost completely (Figs. 5 & 7). Though the maximum length of cod (106 cm) was larger than that of the haddock (75 cm), they did not seem to feed at a higher TL as indicated by their $\delta^{15}\text{N}$ values (Fig. 5). This was surprising as

large cod have been reported to be more piscivorous opportunistic feeders than haddock (Pálsson 1994, Høines & Bergstad 1999). In the adjacent fjord to Ullsfjord, Sørfjord, cod was the dominant predator (Pedersen et al. 2008) and had the highest $\delta^{15}\text{N}$ of the predatory fish species (Nilsen et al. 2008). Pálsson (1994) reported that fish constituted, on average, over 50% of the diet in the North Atlantic cod stocks. In support of this, Dalpadado & Bogstad (2004) investigated cod in the Barents Sea and found that by the age of 2 yr, fish constituted an average 50% of their diet. However, there is also evidence that both haddock and cod can be opportunistic feeders when there are high abundances of other prey. From Ullsfjord, euphausiids and the shrimp *Pandalus borealis* were important prey for cod throughout the year (dos Santos & Falk-Petersen 1989). Høines & Bergstad (1999) concluded that haddock was primarily benthivorous, but when herring *Clupea harengus* eggs were abundant both cod and haddock fed on these. Bogetveit et al. (2008) found that when capelin *Mallotus villosus* was abundant in the Barents Sea, haddock and cod both fed on the high availability of this nutritious food source even if it was only for a short period of time. Our results suggest that large individuals of both species are opportunistic feeders and feed on the same abundant food sources in Ullsfjord. The results show how one species can have very different feeding habits within a limited size range and between geographic areas. The results can be useful when planning food web models as a wide range of fish sizes are not always sampled.

The demersal fish species sampled are the main species in the fjord system with regard to biomass. It was interesting to observe that when we excluded the cod over 45 cm in length, cod had the lowest $\delta^{15}\text{N}$ of the demersal species in the size range 25 to 45 cm. The cod may be using a larger range of feeding niches and feed on, for example, the benthic spider crab *Hyas* sp. (Kanopathippillai et al. 1994) as well as the amphipod *Gammarus* sp. as both species have very low nitrogen signatures (Nilsen et al. 2008). Preliminary diet investigations from Ullsfjord show that cod feed on a variety of crustaceans (data not shown).

The isotope signatures of haddock overlapped closely with those of whiting and long rough dab and partly with those of witch flounder, which means that they prey on similar species in Ullsfjord (Figs. 6 & 7). Many trophic pathways can lead to similar isotope signatures in top predators; it is possible that the resources are split up, but preliminary diet investigations show that euphausiids and shrimp are important prey for many of these species (data not shown).

The stable isotope signature can be used as a quantitative measure of a species' niche because it represents a time-integrated average of all prey species. That many species occupy a similar niche at the same trophic level is a strong indication of trophic redundancy, i.e. a large proportion of species is characterized by similar trophic ecologies (Layman et al. 2007). The euphausiids *Meganyctiphanes norvegica* and *Thysanoessa raschii* are very abundant in Ullsfjord (Zhou et al. 2005) as are the shrimp species *Pandalus borealis* and *Pasiphea multidentata* (data not shown). Therefore, interspecific competition is not necessarily high even if the demersal fish species feed on the same food source.

Haddock in other areas

Haddock is generally assumed to be a benthic feeder (Wainright et al. 1993, Høines & Bergstad 1999, Mente et al. 2008). Diet investigations have shown that haddock feed mostly on benthic invertebrates such as polychaetes, brittle stars (ophiurids) and crustaceans (e.g. Mattson 1992, Albert 1995, Dame & Christian 2008). From the North Sea, haddock feed almost exclusively on benthos and infauna (Schuckel et al. 2010) or nocturnally on sandeel *Ammodytes marinus*, when the burying species in practice becomes a benthic prey (Temming et al. 2004). From the Barents Sea, Jiang & Jørgensen (1996) found that small haddock fed more on crustaceans and annelids but less on echinoderms and fish compared with haddock >20 cm. This is partly in agreement with our results as it showed that haddock changed their diet at the same size as found in our investigations. However, haddock in Iceland prey on deep-water shrimp *Pandalus borealis* and euphausiids when these are abundant (Bjørnsson et al. 2011). The demersally associated diet of haddock is also reflected in the few published isotopic investigations (Table 2). From Icelandic commercial catches, Sarà et al. (2009) found haddock $\delta^{13}\text{C}$ to be -16.6‰ , and from Georges Bank, Fry (1988) found haddock $\delta^{13}\text{C}$ to be -16.3‰ . Both these values were clearly enriched compared with the particulate organic material (POM) from the same investigations (-21.1‰ and -21.3‰ , respectively). POM can be used as a measure of the pelagic carbon, meaning that the haddock in these investigations probably fed on fauna associated with the benthos.

In Sørfjord, the fjord upstream of Ullsfjord, Nilsen et al. (2008) published $\delta^{13}\text{C}$ values uncorrected for lipid content, and after lipid correction by Eq. (1)

Table 2. *Gadus morhua* and *Melanogrammus aeglefinus*. Stable isotope signatures of cod and haddock as found in the literature. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, n and length range given in the literature where both cod and haddock were investigated. na: not available

Area	Cod				Haddock				Reference
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n	Length range (cm)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n	Length range (cm)	
Ullsfjord	-19.6 ^a	13.7	58	10–115	-20.1 ^a	13.0	75	16–75	Present study
Sørfjord	-18.3 ^a	15.3	10	>35	-17.9 ^a	14.8	4	50–53 ^c	Nilsen et al. (2008)
	-18.6 ^a	14.3	4	<35					
Iceland	-17.0	12.8	6	na	-16.6	13.6	4	na	Sarà et al. (2009)
North Sea (southern)	-16.3 ^b	19.2	6	37–95	-16.9 ^b	14.8	1	40	Das et al. (2003)
West Greenland	-18.1 ^b	13.1	13	26–46	-18.0 ^b	13.0	12	18–24	Møller (2006)
	-18.1 ^b	13.1	25	51–64					
	-17.3 ^b	15.5	4	66–70					
Gulf of St. Lawrence	-19.5 ^b	14.6	11	14.5–32	-19.6 ^b	14.7	1	18.5	Lesage et al. (2001)
	-19.2 ^b	15.8	9	33–44.6					
Georges Bank	-16.4	12.6	1	na	-16.3	12.2	2	na	Fry (1988)

^aValues were lipid-corrected using Eq. (1)
^bSamples were chemically treated to remove lipids
^cValues from personal communication with author

using the C:N ratios supplied (M. Nilsen pers. comm.), $\delta^{13}\text{C}$ for the 3 haddock ≥ 50 cm and for the copepod *Calanus finmarchicus* became -17.9‰ and -18.2‰ , respectively. *C. finmarchicus* in Ullsfjord had a mean lipid-corrected $\delta^{13}\text{C}$ of -19.9‰ , and the 1.7‰ higher value in the relative shallow Sørfjord may be due to the contribution to the detritus from kelp and macroalgae that have higher $\delta^{13}\text{C}$ values than do phytoplankton (Fredriksen 2003). The largest group of haddock in Ullsfjord (>50 cm) had a lipid-corrected value for $\delta^{13}\text{C}$ of -19.4‰ and the 1.5‰ higher value for haddock in Sørfjord is similar to the difference between the fjords for the baseline organism *C. finmarchicus*. This indicates that haddock have similar feeding patterns in the 2 fjords.

Most studies of stable isotopes on haddock give one general mean and SD value and do not investigate length groups (Table 2). Sample sizes are also in many cases very small and length range is not included in some papers. Furthermore, haddock under 20 cm are rarely included. The food web in waters of West Greenland was investigated by Møller (2006) and he sampled stable isotopes of haddock in the length group 18 to 24 cm total length and found the $\delta^{13}\text{C}$ of haddock there to be -18.0‰ (SD, 0.3), which suggests a higher proportion of pelagic feeding than has been described in previous literature. One haddock of 18.5 cm was included in the survey in the Gulf of St. Lawrence, Canada, by Lesage et al. (2001) and this haddock had a $\delta^{13}\text{C}$ of

-19.6‰ , a value that was depleted and matched the pelagic shrimp *Pasiphea multidentata* from the same investigation. This may indicate that young haddock in some areas are eating pelagic food, similar to the pattern found in Ullsfjord. Mattson (1992) pointed out that haddock are poorly adapted to eat pelagic food because their mouth is situated sub-terminally. He also claimed that haddock would only eat pelagic food if it happened to be close to the bottom. This does not correspond with our analysis, which suggests that haddock at a young stage feed higher in the water column relative to larger haddock. We cannot see how the $\delta^{13}\text{C}$ signature could be depleted unless significant parts of their diet came from the pelagic food web over a long period of time. It is possible that because of high predation pressure as well as competition from other large demersal species in the near-bottom habitat, the small haddock have adapted to searching for food higher in the water column and this is an example of intraspecific, size-dependent niche diversification and ontogenetic niche change. This adaptation can possibly increase survival of small haddock.

Our investigation in Ullsfjord covered a large range of length groups of cod and haddock. We propose to use stable isotopes to investigate feeding changes and when building food web models as differences in feeding preference and ontogenetic niche changes are essential to understanding food web ecology.

CONCLUSIONS

Haddock have an ontogenetic shift in stable isotope signatures that reflect a shift in diet from pelagic to benthic prey shortly after growing to 20 cm in length. Atlantic cod have a gradual change from a partly pelagic to a more benthic diet as they grow. Small haddock seem to have a diet that is very different from both large haddock and small and large cod. Several large demersal fish species seem to be at a similar trophic level in Ullsfjord as indicated by their $\delta^{15}\text{N}$ and their $\delta^{13}\text{C}$ signatures, which overlap and thus show a strong indication of trophic redundancy.

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